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VI.

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY.

XIII. — NOTES ON ZONARIA VARIEGATA, LAM'X.

By Herbert M. Richards.

Presented by W. G. Farlow, June 11, 1890.

Late in the year 1889 I began working on a quantity of material of various forms of the Dictyotaceæ which Professor W. G. Farlow had kindly placed at my disposal. The specimens had been collected by him in Bermuda during January, 1881, and were in excellent condition for histological study. Among the first forms I examined, in some material of *Zonaria variegata*, Lam'x,* a curious structure attracted my attention, to which no reference could be found in the accessible literature on the subject. A description of this peculiarity and its mode of origin is the subject of the present paper.

At the outset, it will be well to review briefly some of the most important features in the structure of the Dictyotaceæ, which have been described by previous writers. Of the literature on this subject Naegeli's description† is among the earliest; later a paper was published by Cohn,‡ in 1865, which included a description of *Dictyota dichotoma*, Lam'x. In Bornet and Thuret's "Etudes Phycologiques,"§ besides a brief description of the frond of *Dictyota dichotoma*, there are especially important notes on the fructification illustrated by beautiful figures. The latest as well as the most elaborate paper on the group, however, was published by Reinke in 1878.¶ There he described, in considerable detail, the structure and development of certain of the Dictyotaceæ found in the Bay of Naples. In general, it may be said that the Dictyotaceæ are thin, flat, membranaceous, olive-brown algæ, usually very simple in structure, having tetraspores, antheridia, and certain large ovoid bodies termed by Reinke, Hauck, and others oogonia. In the fronds of the various genera of this group two forms of growth may be distinguished; one by means of a single apical cell, of which Dictyota is a type, and another by means of a row of marginal cells of which Padina affords a good example. While at first it would seem that these two methods of growth are widely different, closer examination shows that the growing marginal cells practically represent a row of apical cells.

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* The reader should consult J. G. Agardh's account of Zonaria in Lunds Univ. Arsskrift, XVII. 120–131, for the relations between this species and its allies.

† Die neuern Algensysteme, Zurich, 1847.

‡ Ueber einige Algen von Helgoland, Leipzig, 1865.

§ Etudes Phycologiques, Paris, 1878; also Thuret, in Ann. Sci. Nat., Sér. III. Vols. XIV. and XVI.

¶ Entwickl. Untersuch., v. d. Dictyotaceen, etc., Nova Acta, Band XL. Part 1, 1878.

The apical growth of *Dictyota dichotoma*, from the formation of the first division to the ultimate condition found, was clearly described by Naegeli, and further details were given by Cohn and by Reinke. From the lenticular apical cell a saucer-shaped cell is cut off by the formation of a transverse wall. This latter cell divides into several by the formation of vertical walls, and later each one of the new cells is cut into three parts by walls parallel to the surface of the frond. Thus the three-layered condition of the adult frond is attained, and the subsequent changes consist chiefly of the division of the outer cells into many parts to form a cortex.

Padina, growing as it does in most European waters, has been abundantly studied, and was for this reason cited as an example of the marginal form of growth, but it differs from other Dictyotaceæ in that the edge of the frond is inrolled. The growing cells which form the margin of the frond of *Padina Pavonia*, Lam'x, may roughly be said to be brick-shaped, with their anterior faces rounded, and their longitudinal axes placed at right angles to the margin of the frond. From them, as in the case of the apical cells in *Dictyota dichotoma*, cells are cut off by the formation of transverse walls. These newly formed cells almost immediately divide horizontally into two parts, one of which grows in area, the other in thickness, so that the edge of the frond gradually curls over on itself, until the inrolled condition is attained. For a considerable space the frond is but two layers of cells in thickness, for the third layer, which is formed by the division of the thicker layer parallel to the surface of the frond, does not make its appearance at once. The increase in breadth takes place from the longitudinal division of the marginal cells, an occurrence that is very common in a young, rapidly growing frond. Besides the large, thin, fan-shaped form of the thallus of Padina usually found, Reinke also distinguished what he terms Rundtriebe and Flachtriebe, which are interesting as showing the close connection of the apical and marginal forms of growth. The Rundtriebe and Flachtriebe resemble each other closely, both having the apical form of growth, differing only in that the former are round, while the latter, as the name implies, are more or less flat. The change from the Flachtriebe to the Breittriebe, as Reinke terms the expanded form of the frond, is accomplished by a change in the mode of growth. Actively growing marginal cells, like those already described, become differentiated from the cells bordering the edges of a Flachtrieb, and the apical cell is obliterated. A very characteristic feature of the expanded form of Padina, and one that should not be passed over, is the hairs which beset both surfaces of the frond. They occur in prominent and regular concentric lines, and are developed from the outgrowth of the superficial cells.

In *Taonia atomaria*, Ag., we have perhaps a more typical form of those genera where the growth is marginal. For a detailed description one should refer to Reinke's paper already alluded to. A few words regarding it will suffice here. In the structure of the frond it differs mainly from Padina in two features; the edge of the frond is not rolled inwards, as in the latter genus, and the hairs, instead of being in definite parallel lines, are in more or less irregular zones. Besides *Taonia atomaria*, Reinke describes another Mediterranean form, with a flat and not incurled margin, which he considers to be *Zonaria parvula*, distinguishing it, however, from the so called *Zonaria parvula* of some older writers, now included in *Aglaozonia reptans*, one of the Cutleriaceæ. The frond of *Z. parvula* is thin, flat, more or less irregularly expanded, and on its under side beset with rhizoid-like hairs, which attach it to the substratum. The growth is by marginal cells, as in Padina, but it resembles Taonia in having the edge of the frond flat. Usually the thallus is but three cells in thickness, consisting of a single-layered, small-celled cortex on each side of the frond, and of a large-celled internal portion. The latter layer, while it is usually only one cell in thickness, may in places become divided into several layers. The growth of the frond from the marginal cells is very much as in Padina, except that both of the cortical layers are formed simultaneously.

The reproductive organs, while they differ considerably in their arrangement in the various genera, are much alike in structure. They are all outgrowths of cortical cells. The development of the tetraspores is as follows. A group of cortical cells becomes considerably enlarged, taking on at the same time a dark brown color. Basal cells are cut off from these enlarged cells by the formation of walls parallel to the surface of the frond. The upper cells then rapidly become very much larger, and when they have attained their full size their contents divide into four spores, which on escaping may develop into new plants. There may or may not be a cuticular envelope covering the tetrasporic sorus in its young stages. In Dictyota the spores are found strewn irregularly over both sides of the frond. In Padina and Taonia they develop on the upper side in the region of and following the same general course as the trichomes. In Zonaria, again, the arrangement is irregular, but the sori are more compact than in Dictyota. While in a majority of cases the oogonia and antheridia are found on separate fronds, in Padina they occur together. The oogonia develop very much in the manner of the tetraspores, by an enlargement of the cortical cells; their contents, however, do not divide into four, but remain as a single mass. The antheridia differ considerably from the oogonia and tetraspores in their growth; the cortical cells after becoming somewhat elongated lose their color entirely, and then by a series of divisions in three directions are cut into many cells, in which the antherozoids are formed.* In Dictyota, which is one of the diœcious forms, the oogonia and antheridia are found in sori scattered irregularly over both sides of the frond. In Padina they occur in zones situated on each side of the concentric lines of hairs. Of these zones the oogonia constitute by far the greater part, being in large masses separated at irregular intervals by narrow spaces of antheridia. Taonia like Dictyota is diœcious, and the oogonia and antheridia are found as in the latter genus. In Zonaria tetraspores alone are known.

In a few words, then, Zonaria may be distinguished from Padina and Taonia as follows. The absence of the inrolled margin is sufficient to separate it from Padina, while the absence of any distinct bands of hairs and the consequent position of the reproductive organs distinguish it, though not so distinctly, from Taonia. It is true that most species of Zonaria are marked with concentric lines, but the lines are rather zones of growth than bands of trichomes. It is indeed concerning these zones of growth that I propose to speak later, but it will be necessary before discussing them to trace the growth and general histological structure of the frond.

Zonaria variegata, Lam'x,* was the form used in the following investigation, and the material, as I have already said, was collected by Professor Farlow in Bermuda. From dried specimens the frond is seen to be more or less fan-shaped, though not so markedly as in Padina, for it is attached by a broader base. When young the frond is prostrate, being fastened to the substratum by the rhizoid-like hairs on its under surface. As the frond becomes older, however, it is often erect, for the hairs break away except at the base, and few new ones are formed on the growing parts. The adult frond is somewhat rigid, not as much so indeed as that of Padina, for there is no incrustation of calcic carbonate, as in the case of the latter. The surface of the frond is marked with fine striations, running lengthwise along the frond, which can be faintly seen with the naked eye and plainly with a hand lens. Running in the opposite direction one can see, at considerable intervals, very strongly marked concentric lines. In its histological structure, *Z. variegata* resembles *Z. parvula* to a considerable extent, differing mainly in the number of layers of cells of which it is composed. There is a row of the same brick-shaped marginal cells with rounded apices as found in the other species (Fig. 1). These marginal cells are cut into two unequal parts by the formation of a series of transverse walls. The larger and upper ones — if we consider the frond in its erect position — continue their office of enlarging the frond, while the lower ones become merged with the rest of the frond. These lower cells soon divide into three parts, by the formation of two walls parallel to the surface of the frond in each cell, thus making an inner and two outer layers. Later, more cells are cut off from the central layer in the same direction as those first formed, until what may be termed a cortex is formed, which may be from two to four cells in thickness (Fig. 2). It must be borne in mind, however, that while these layers thus formed will, to avoid confusion, be hereafter called the cortex, one cannot well say where the cortical cells end and the medullary cells begin, for as far as the color and character of the contents go there is a gradual transition from one to the other. The color of the contents of the outside layer is dark brown, that of the next somewhat lighter, until in the medullary layer they are almost colorless. The outermost layer not long after its formation divides up by transverse and vertical walls into many small cells. The same division takes place in the next layer to a lesser extent, but the others remain as they were when first formed. Thus in a fully developed portion of the frond, beginning at the inside and going outwards, there is first a large-celled central layer, then from one to two layers of large flat cells, which, with the two outer small-celled layers, may be said to constitute the cortex. In the young thallus the margin is entire; but it soon becomes split, though to a less degree than in some species of Zonaria. The splitting takes place by a process very like that described by Reinke in the case of *Taonia atomaria.* Usually a small number of the marginal cells die, and their contents disintegrate, forming a brownish structureless mass. Since the marginal cells on either side continue to grow, there is formed a cleft, which gradually grows deeper and deeper, finally forming a split which becomes visible to the naked eye.

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* Thuret, Ann. Sci. Nat., Sér. III. Vols. XIV., XVI.

It was in a vertical longitudinal section of the frond which I had cut to study the apical growth, that a peculiar appearance like that shown in Figure 2 was seen. This occurred to me at once as strange, and unlike anything I had seen before. No reference to any such condition could be found in the literature on the subject, and, unless I am greatly mistaken, it has never been mentioned. This singular condition when fully formed may be briefly described as an overlapping forward of the cortical cells over the frond. That to this overlapping the appearance of transverse zones is due, becomes evident on viewing it with a low power from above, when the lines of the projecting cortical cells may be seen at more or less regular intervals. These zones should not be confounded with the comparatively fine and indistinct lines which run parallel to them, and are only to be seen on viewing the frond obliquely. The latter markings are apparently due to slight undulations of the cortical cells, while the zones referred to are much more complicated in structure. In a vertical section of the zones in their fully formed condition the most prominent feature are the outgrowths on both sides of one or two layers of the cortical cells. But besides this, it is seen that in the region of the zonal growth the medullary cell has become divided into three or four parts horizontally, and that the whole frond in that place is somewhat thickened (Fig. 2). The earliest stage in the development of these zones that I was able to find in the material at hand was young enough to give pretty clear evidence as to their origin. In this stage the medullary cells in the region of the zone about to be formed became divided into three or four cells by the formation of longitudinal walls parallel to the surface of the frond (Fig. 3, m'). The medullary cells which undergo division in this way form usually a single row parallel to the margin of the frond, but occasionally, instead of a single, they consist of a double row (in Figs. 3 and 4 the direction of the margin of the frond is indicated by the letter A). At the same stage the cortical cells (Fig. 3, *c*) in the immediate neighborhood of the developing zone can be seen to have undergone a change. The two outermost layers if there are three or four in the frond, or the single outer one if there are only two, have begun to disintegrate (Fig. 3, *c'*). These cortical cells have lost their definite shape, the walls between them having undergone a process of absorption. This absorption has not progressed so far, however, that traces of the original outline of the cells cannot still be seen in the stage figured (Fig. 3, *d*). The contents have also much altered, becoming in the process of disintegration a dark brown color. The absorption and degeneration continue, and finally even the outer cell wall is broken away and the now structureless mass of contents escapes as is shown in Figure 4, *c'*. Other changes have also taken place. The cells composing the layer next inside the disintegrated cortical cells have enlarged somewhat (Fig. 4, *ic*), and on looking at the medullary cells, which in this region it will be remembered have increased in number, it will be seen that their anterior, or marginal, ends have become thicker, so that the cells are more or less wedge-shaped. The frond has thus become so enlarged, that the cells of what I have called the innermost layer of the cortex are so displaced that, while posteriorly (B) they retain their connection with the layer of which they are in reality a part, anteriorly (A) they appear to be continuous with the outer layer of the cortical cells of the younger part (Fig. 4, *ic*). The cortical cells just posterior to the zone of disintegrated cells described have begun to grow forwards, and their course being somewhat divergent they turn outwards, finally forming the overlapping ridges (Fig. 2) which give the zoned appearance to the surface of the frond. The cortical cells do not grow on indefinitely, but usually project only the length of a few cells, sometimes, however, growing farther (Fig. 2). As regards the relative stage of development of these zones on various parts of the frond, it may be said that the early stages are always found near the margin of the frond, and, while fully developed ones are sometimes met with close to the edge (Fig. 2), one must look for the oldest farther back.

The nearest reference that can be found to anything approaching the condition described in this curious overlapping, is in Reinke's description of *Z. parvula*, where he says that not infrequently the middle layer was found to be divided irregularly;* but he does not speak of the formation of zones in this connection, nor does he mention any other of the changes that I have described.

The part which the overlapping takes in the economy of the frond is a point concerning which only conjectures can be made at best. It does not seem to be connected in any way with the formation of either the reproductive organs or the hairs. One might suppose that the different zones represent successive periods of growth and rest. For instance, the zonal outgrowths may represent a point where the growth of the marginal cells was checked, and where, after a period of quiescence, they began growing again suddenly. What the cause of such a cessation and subsequent resumption of growth might be, is a question which cannot be decided without carefully observing the conditions of growth of the plant. It is to be regretted that the plant could not have been studied in the living state; but that was of course impossible, owing to the remoteness of its habitat.

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* Entwickl. Untersuch., v. d. Dictyotaceen, etc., p. 35, Taf. VI. Fig. 4.

Of the hairs in *Zonaria variegata* two kinds may be distinguished, those which occur in tufts scattered irregularly over the frond, and those which are rhizoid-like in their nature, and are found chiefly near the base on the under side of the frond, not arising in compact tufts like the others. The hairs in the tufts are always unbranched, and are composed of long cylindrical cells placed end to end. They develop from the elongation of a group of cortical cells, and are in the young stages protected by a covering which subsequently breaks away, as described by Naegeli in the case of *Padina Pavonia.* The rhizoid-like hairs resemble those which develop in tufts in that they are outgrowths of the cortical cells, but they differ in that they are scattered irregularly over a considerable area. They may also be distinguished by the greater length of their component cells and by the fact that they are branched (Fig. 5). While they are usually developed only near the base of the frond, they may occur to a limited extent anywhere on its under surface.

The reproductive bodies which I found on the frond of *Zonaria variegata,* although no division into four parts was seen, were presumably young tetraspores. As Bornet has remarked,* however, it is very difficult to distinguish the tetraspores from the so called oogonia unless the division of the former into four parts is seen; and although apparently not a difficult matter to detect the four tetraspores in living material, in dried or alcoholic material the mother cell of the tetraspores often appears to be undivided. They arise from the enlargement and division of groups of epidermal cells, and are protected in their young stages by a covering like that found in the case of the hairs. They were not at all definitely arranged, being scattered irregularly in patches between the overlapping zones.

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* Etudes Phycologiques.

In examining some material of *Dictyota ciliata* which was collected at the same time and place as that of *Zonaria variegata*, I came across an interesting point regarding the tetraspores to which it seems worth while to call attention. The tetraspores in the material examined were apparently not fully developed, at least no typical division into four was seen. Very often, however, a vertical wall divided the upper cell of the tetraspore in half (Fig. 7), which was presumably preparatory to dividing again at right angles to form the quadripartite condition usually found. But this simple bisection was not the only form of division observed. Frequently irregularly placed walls were found which were not compatible with a division of the spore into four parts. In Figure 8, an extreme case is shown. There are apparently two basal cells, somewhat distorted, and in the tetraspore itself, starting from a central cell are several radial septa which divide the spore into a considerable number of parts. The septa were not always to be reduced to such a definite plan; there were several cases like those shown in Figures 9 and 10, where the divisions were so irregular that no order could be found in their arrangement. The significance of this multiple division could not be explained with only alcoholic material; it was too frequent, at least in the specimens I examined, to be an accident. A study of the living plant would be necessary to determine certainly if these bodies were really tetraspores, and not some form of gemmæ.

In conclusion, I wish to express my great indebtedness to Professor Farlow, not only for the use of his material, but also for his kind assistance throughout the course of my work. To Mr. W. S. Wadsworth I am also obliged for specimens of *Zonaria variegata* sent by him from Bermuda.

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Harvard University.

EXPLANATION OF FIGURES.

ZONARIA VARIEGATA.

Fig. 1. Small portion of edge of frond showing marginal cells. Surface view. × 83.

Fig. 2. Vertical section near margin of the frond showing a well developed overlapping zone. × 200.

Fig. 3. Vertical section near margin of frond showing a very young stage in the development of overlapping zone. A indicates the direction of the margin, B indicates the direction of the base.

m, medullary cell.
c, cortical cell.
m′, divided medullary cells.
c′, disintegrating cortical cells.
d, remains of walls of cortical cells. × 350.

Fig. 4. Same as Fig. 3, but older stage.

ic, internal cortical layer, which is here pushed aside. × 350.

Fig. 5. Rhizoid-like hair. × 83.

DICTYOTA CILIATA.

Fig. 6. Undeveloped tetraspore. × 200.

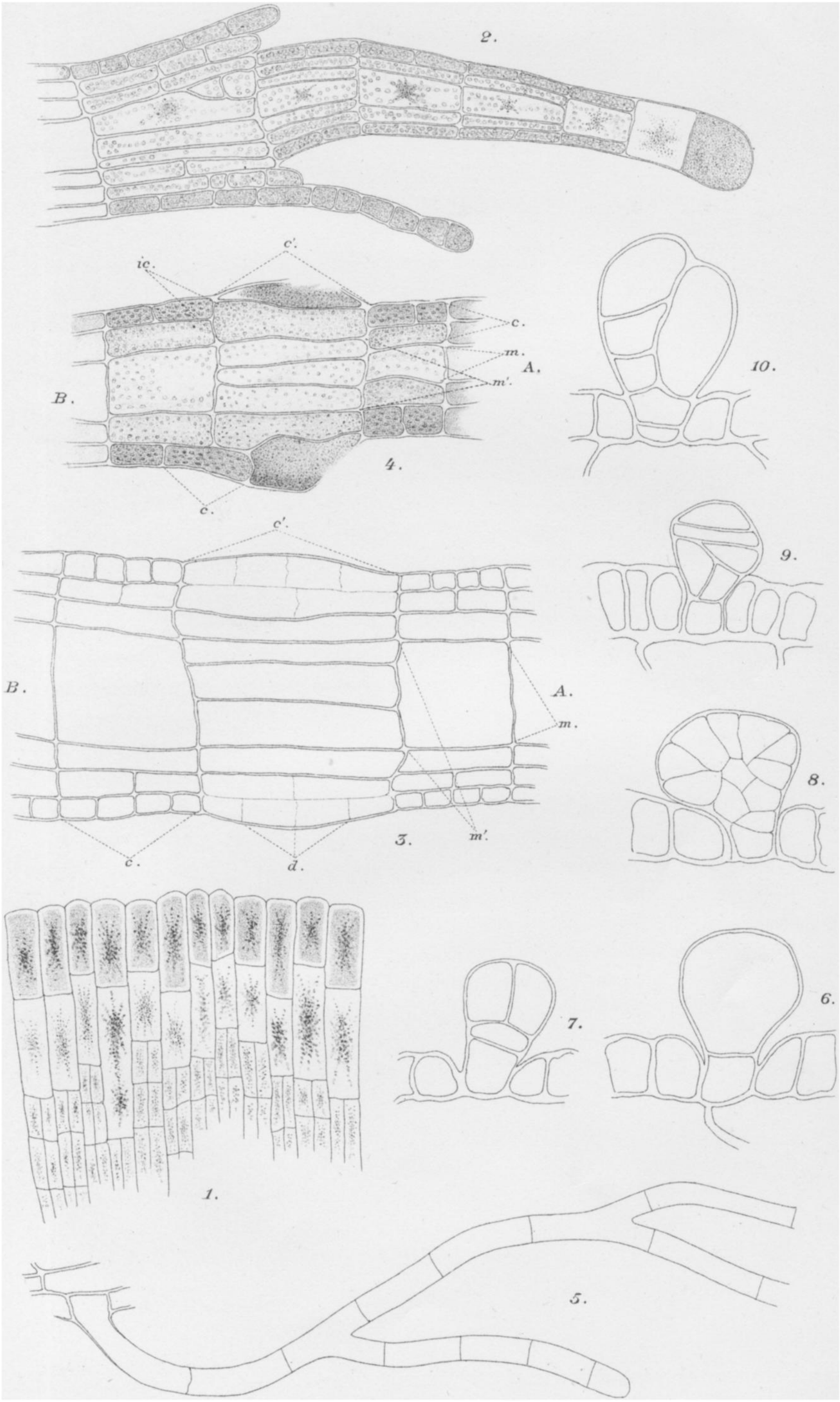
Fig. 7. Tetraspore with two basal cells showing simple bisection. × 200.

Fig. 8. Tetraspore showing radial divisions. × 200.

Figs. 9 and 10. Irregularly divided tetraspores. × 200.

All the figures were drawn with the aid of the camera lucida. From the drawings thus made Figures 3, 4, and 5 were reduced one third; the others remain as they were drawn.

Richards – Zonaria variegata.



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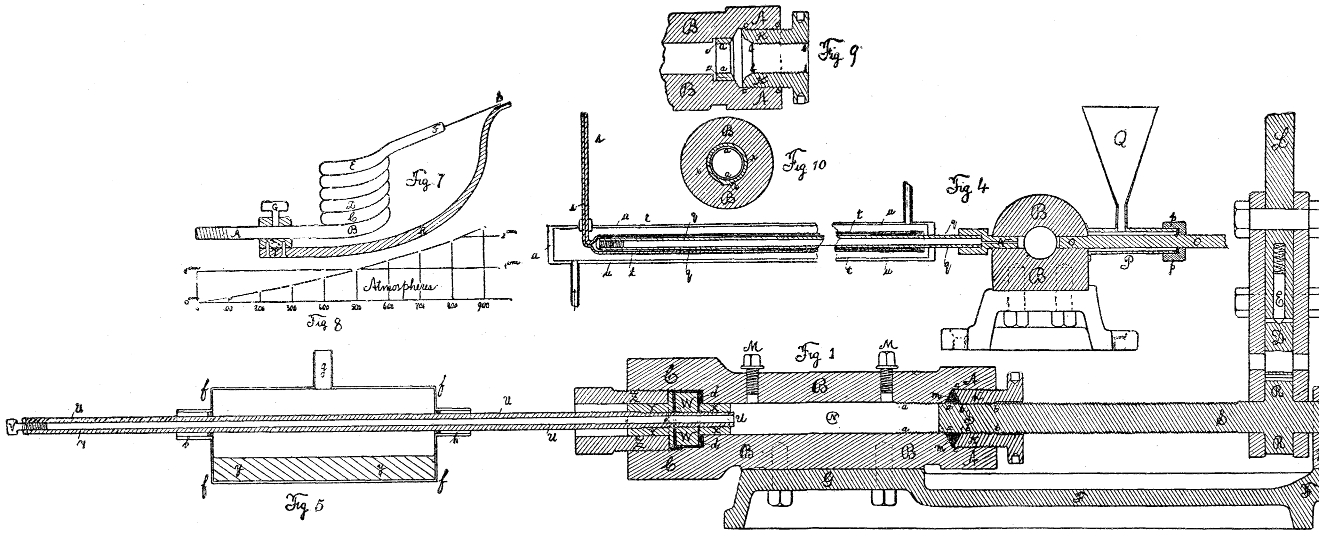
B. Meisel. lith.

THE SCREW COMPRESSOR.



Scale 1 in. = 6 inches.

Fig. 1. — Longitudinal section of the screw compressor, showing the barrel, screw, and lever. Scale $\frac{1}{6}$.

Fig. 2 — End elevation, showing shaft of screw.

Fig. 3. — Longitudinal section of the lever and ratchet wheel. Scale $\frac{1}{6}$.

Fig. 4. — Cross section of the screw compressor, showing the gauge and the oil supply in longitudinal section. Scale $\frac{1}{6}$.

Fig. 5. — Longitudinal section of the piezometer tube and the vapor bath. Scale $\frac{1}{6}$.

Fig. 6. — Chart showing the bow-shaped cycl

Fig. 7. — Direct reading, spiral Bourdon gaug

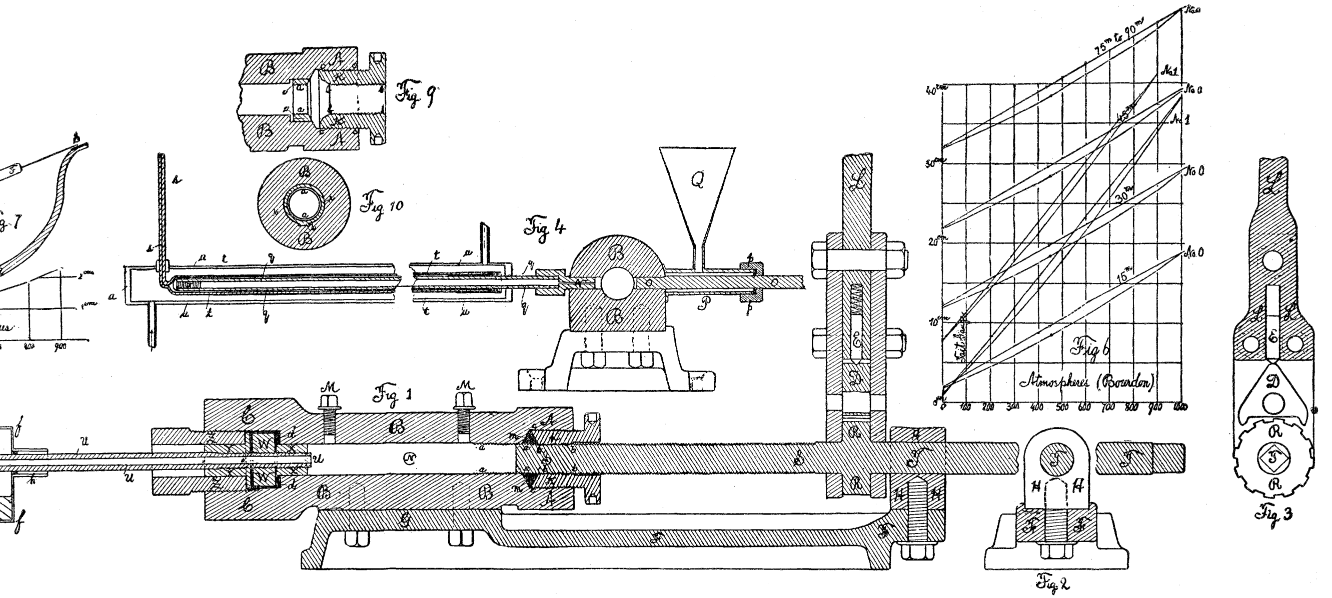
Fig. 8. — Chart showing the action of the san

Fig. 9. — Longitudinal section of the impro

sion. Scale $\frac{1}{6}$.

Fig. 10.—Cross section of the barrel showing

THE SCREW COMPRESSOR.



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d ratchet wheel. Scale $\frac{1}{6}$.

sor, showing the gauge and the oil supply in

ter tube and the vapor bath. Scale $\frac{1}{6}$.

Fig. 6. — Chart showing the bow-shaped cycles obtained in the gauge comparisons.

Fig. 7. — Direct reading, spiral Bourdon gauge. Scale $\frac{1}{6}$.

Fig. 8. — Chart showing the action of the same.

Fig. 9. — Longitudinal section of the improved stuffing box for high pressure compression. Scale $\frac{1}{6}$.

Fig. 10.—Cross section of the barrel showing the ring. Scale $\frac{1}{6}$.